

**BREEDING HABITS OF THE
FREE-TAILED BAT**

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This is a dissertation submitted in partial fulfillment of the requirements for the
degree of Doctor of Philosophy in the University of Michigan

1937



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The breeding habits of the free-tailed bat of the southeastern United States, *Tadarida cynocephala* (Le Conte), have been investigated as a part of a study of the life history of this species. These bats are locally abundant in Florida, and in some places large colonies of them occur in buildings. For many years a colony has occupied parts of an old building in Gainesville, and this is the source of all of the material herein discussed.

For assistance in this work I wish to make the following acknowledgements: The Museum of Zoology of the University of Michigan granted me a fellowship, the use of its library, and numerous other facilities; the suggestions of L. R. Dice were particularly valuable. In addition, the Department of Zoology of the University of Michigan furnished me with laboratory facilities for microtechnique by means of which I made many of the slides mentioned later. On two occasions A. F. Carr and Dr. Wesley Clanton collected specimens for me at a time when I was unable to do so. For the aid received from these sources I wish to express my indebtedness.

The section of the building where these bats roost (fig. 1) is used primarily for the storage of fertilizer. The bare rafters and rough board partitions of these poorly lighted rooms furnish suitable quarters for this species, as shown by the fact that more than 10,000 individuals usually are present from June

until early autumn. At the top of the partitions, a series of crevices are favorite retreats. These are about one foot in vertical extent by one inch in depth, and vary in width from 3 or 4 inches to as much as 2 feet. The only other species of bat that I have found here is *Myotis austroriparius* (Rhoads), individuals of which are present only occasionally and in relatively small numbers.

The number of *Tadarida* in the building decreases as the weather becomes colder in the autumn, although several hundred usually are present throughout the winter months. The severe winter of 1934–1935 was exceptional in this respect, for only a few bats were present in the building during the coldest weather. Few or no bats were found in the building for about a week in March throughout a seven-year period, 1929–1935, and evidence presented later indicates that copulation occurs at this time. Nearly all of the bats found in the building at this time are immature males.

When the bats return, nearly all of the females are pregnant. The earliest date on which I have evidence of ovulation in this species is March 17. Two adult females captured March 15, 1934, were kept in an unheated room for 2 days before they were dissected. Serial sections of the reproductive tract of 1 of these individuals show a partly formed corpus luteum in the right ovary and an egg in cleavage, consisting of 2 cells, (figure 2) in the right tube. Ovulation had not occurred in the other individual nor in 5 adult females taken March 7, 1933. Ovulation had occurred in 18 bats of this species taken March 23, 1929. At least 16 of these contained embryos ranging in development from morulas in the tube to embryos in the uterus with germ layers differentiated. Sections saved of the other individuals show no embryos; but these series are incomplete. The presence of a corpus luteum in the right ovary of each of these 2 specimens shows, however, that ovulation had taken place. From early April to the first of June non-pregnant females of this species were very rarely found.

The time of ovulation in the *Tadarida* of the colony studied is quite restricted, judged by the dates when young were born and by the measurements of embryos taken on a single date. It is generally understood that fertilization in mammals takes place soon after ovulation and all recent authors agree that embryological development of bats ensues at once after fertilization is accomplished, thus disagreeing with the theory of Van Beneden (1875) that development is delayed with some species of bats for several months after the fertilization of the ovum. For these reasons, and assuming that the period of gestation is constant, the extent of the time of parturition and the size of embryos furnish reliable evidence as to the duration of the time of ovulation.

The earliest date of parturition in *Tadarida cynocephala* for which I have evidence is May 31, 1929. One of the 10 females taken on this date had recently given birth, as indicated by the greatly enlarged but empty uterus.

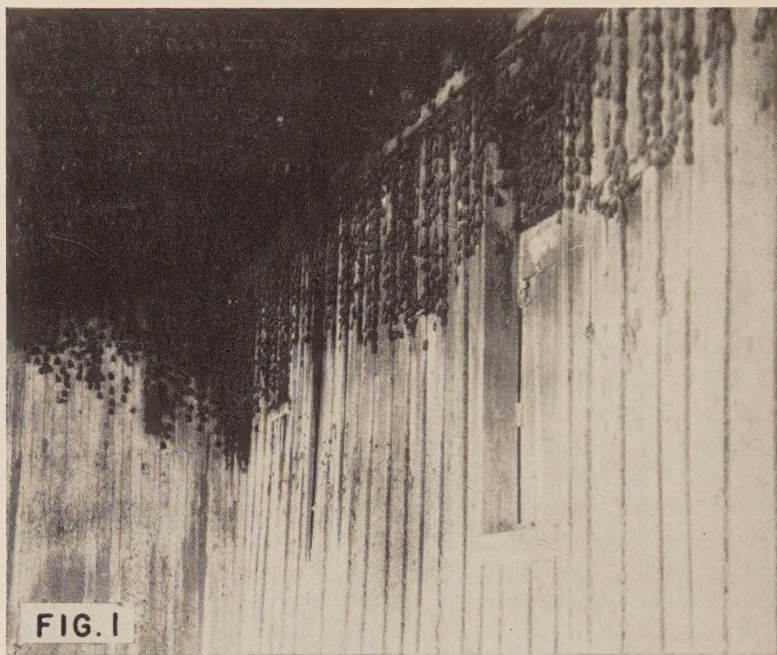


FIG. 1. A portion of the colony of *Tadarida cynocephala* under discussion, photographed September 7, 1931.

FIG. 2. Section of a segmented ovum of *Tadarida cynocephala* in the fallopian tube of a specimen taken March 17, 1934.

I was unable to find young among the colony on this date, however, or on June 2, although many were present June 3. Most of the young, estimated to be about 4000 in this colony, had been born by June 11, 1929, for on this date many females were captured before a pregnant specimen was found.

In 1931, the time of parturition was about a week and a half later than in 1929, as shown by the following observations. The majority of the adults of this species leave the building a few minutes after sundown, but fail to take their young with them. A thorough examination of the building after most of the bats had left on the night of June 10, 1931, resulted in finding no young. Three nights later, 350 young were counted in or near 19 of the crevices at the top of a partition, which is the place where nearly all of the very young bats of this colony were found. On the night of the 15th, 567 young bats were counted, while on the night of the 17th, at least 1459 young were present. It seems certain that many more were not seen, however, as they were crowded together and retreated into the crevices at the approach of the light. On none of these occasions were the young removed from their resting places. On June 24 of the same year most of the young had been born, and 4 days later several hundred females were captured before a single pregnant specimen was obtained. On June 29, 1931, no pregnant females could be found in the colony during a search of two hours. The pregnant female captured June 28 gave birth to a young one on June 30, 1931, which is the latest date for which I have evidence of parturition in this species.

It is thus evident that nearly all of the young *Tadarida* were born within an interval of 2 or 3 weeks, from May 31, or a day or two earlier, to June 11, 1929, and from June 13, or a day or two earlier, to June 30, 1931.

The lengths *in utero* of all of the larger embryos of this species taken in 1929 are indicated in figure 3. The smaller embryos, all of which were taken before April 8, were not measured. With the exception of a 3.5 mm. embryo taken April 23, there is no great variation in the size of embryos taken on the same day. The extremes in size of embryos taken April 23 (3.5 to 14.5 mm.), in comparison with the size of embryos taken on other dates, seems to indicate a difference in age of about 3 weeks. The relatively small amount of variation in the size of other embryos taken on the same day is apparently due to a difference in age of but little more than a week, as shown by comparing the size of the largest embryo taken on a certain day with that of the smallest embryo taken a week later.

All of the larger embryos taken on the same day in 1930, indicated in figure 3, show about the same amount of variation in length as those taken in 1929, but parturition occurred at about the same time in 1930 as in 1931 and the embryos are correspondingly smaller in the 1930 series than those taken on a corresponding date in 1929. June 12 is the earliest date that young were found in 1930. Thus the extent of the time of parturition and

the size of embryos taken on the same day indicate that ovulation occurs with virtually all female *Tadarida* of the colony studied within an interval of 3 weeks in one year, and in 9 out of 10 cases it probably occurs within an interval of but little more than a week. In different years the duration of the time of parturition, May 31 or a day or two earlier, to June 30 in 1929 and 1931 respectively, indicates that in this colony ovulation takes place during an interval of about one month.

The time required for the development of the various stages of small embryos of *Tadarida cynocephala* is unknown. It seems probable, however, that 2 morulas, a single one found in the right fallopian tube of each of 2 specimens taken March 23, 1929, are less than a week old. Such being the case the preceding evidence indicates that ovulation and fertilization oc-

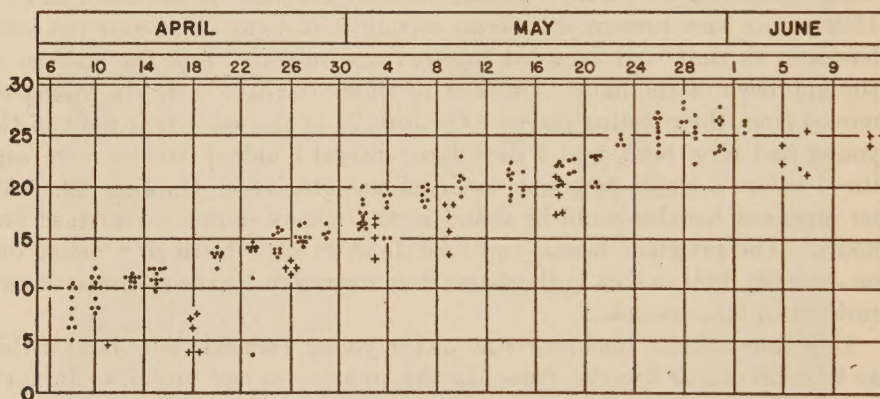


FIG. 3. Length *in utero* of embryos of *Tadarida cynocephala*, measured in millimeters. Those taken in 1929 are designated by dots, and those taken in 1930, by crosses.

curred in most of the *Tadarida* of this colony during the second and third weeks of March in 1929, and about one and one-half weeks later in 1930 and 1931. March was colder in 1930 and 1931 than in 1929, and this possibly is the reason for the later dates of ovulation in these years.

The period of gestation in this species, judging from the evidence here presented, is between 11 and 12 weeks.

It is of interest to note that, relative to the time of ovulation, large ovarian follicles are present in these bats in all months of the year. The number of vesicular follicles, determined by means of serial sections, found in both ovaries of specimens taken in all months of the year, is given in table 1. This evidence shows that the only time when large follicles are uniformly absent is when small embryos are present. The vesicular follicles are mostly present in the right ovary only, but 4 of these were found in the left ovary of 1 specimen, 2 in 2 other specimens, and 1 in each of 7 others from a total of 82 individuals.

TABLE 1

COLLECTION DATE		NUMBER OF VESICULAR FOLLICLES PRESENT IN BOTH OVARIES	NUMBER OF SPECI- MENS	EMBRYO IN TUBE	EMBRYO IN UTERUS	EMBRYO A MORULA STAGE OR YOUNGER
January	17	8, 10, 11	3			
	20	10, 12	2			
	29	17	1			
February	5	17	1			
	15	15, 24	2			
March	7	6, 11, 11, 12, 13	5			
	17	12	1			
	17	0	1	x		x
	23	0	1	x		x
	23	0, 0, 0, 0, 0, 0, 0, 0, 0, 0	11		x	
	24	0, 0	2	x		x
	24	0, 0, 0, 0	4		x	
	24	10	1		x	
	26	0	1		x	x
	26	6	1		x	
April	1	8	1		x	
	4	3	1		x	
	11	3, 7	2		x	
	18	7, 9, 10, 13	4		x	
May	7	0	1		x	
	10	0	1			
June	18	11	1			
	25	6	1			
July	14	0, 1	2			
	24	4, 5	2			
August	7	1, 5	2			
	17	10	1			
	28	7	1			
September	8	19	1			
	19	8	1			
	30	3, 5, 5, 13	4			
October	14	9, 13, 16	3			
	17	8, 8, 10	3			
	24	7	1			
November	8	2, 2, 4, 4, 6, 8	6			
	12	14, 20	2			
December	10	11, 11, 12	3			
	23	17	1			

That all but 1, or rarely 2, of these large follicles atrophy without the occurrence of ovulation is shown by the fact that only 1 corpus luteum was found in the right ovary of 30 specimens, and in 1 specimen 2 were present. None was found in the left ovary. All of the specimens in which corpora lutea were found were taken during the time of gestation, from the middle of March to early June.

Spermatozoa were found in the female reproductive tract of but 5 of the many specimens examined. These were captured February 13, 1932; February 27, 1932; 2 specimens March 7, 1933; and the fifth specimen March 23, 1929. Of these 5, ovulation had taken place only in the specimen taken March 23, and this individual contained an embryo with the central cell mass somewhat separated from the trophoblast. This indicates that mating occurs, in various years, during a period of somewhat more than 5 weeks and at about the time of ovulation in the *Tadarida* of the colony studied, and that spermatozoa are not stored in the female reproductive tract of this species of the Molossidae as is known to be the case for several species of the Vespertilionidae and Rhinolophidae. For a review of the literature dealing with the survival of spermatozoa in the genital tract of bats, see Guthrie, 1933; Hartman, 1933; Hamlett, 1935; and Gates, 1936.

In this species the embryo nearly always develops in the right horn of the uterus. A single embryo was found in the right horn of each of 300 pregnant females examined and in only 1 individual was it in the left horn.

Females of this species apparently reach maturity during their first year, as shown by a banded individual. Seventy-six young *Tadarida* but a few days old were banded in this colony June 7, 1929. On April 11, 1930, a banded female which contained an embryo, was taken. The band of this individual is greatly worn and the number is illegible. The teeth also are greatly worn, presumably due largely to their use in trying to remove the band, for I have seen some of these banded *Tadarida* bite the bands attached to the legs. There seems to be no reasonable doubt, however, that this is one of the young banded the previous June, for under date of July 9, 1931, Frederick C. Lincoln of the Bureau of Biological Survey, from which source the bands were secured, wrote me that no one else to his knowledge had banded any free-tailed bats in the eastern United States. For these reasons it seems evident that female *Tadarida cynocephala* are mature their first year, at the age of about 9 months.

A periodic sexual development is known to occur annually in the males of some species of bats in which the time of ovulation is probably well defined. An extensive account of the reproductive cycle of males of several species of bats of western Europe was given by Courrier (1927). He had many specimens, taken at various times of the year, of *Vesperugo pipistrellus* (= *Pipistrellus pipistrellus*, Miller, 1912), *Miniopterus schreibersii* and *Vesperugo serotinus* (= *Eptesicus serotinus*, Miller, 1912) and less adequate series of

Vespertilio murinus (Schreber) (= *Myotis myotis*, Miller, 1912), *Vespertilio capaccinii* (= *Myotis capaccinii*, Miller, 1912), *Plecotus auritus*, *Rhinolophus ferrum-equinum*, and *R. hipposideros*.

He showed that spermatogenesis occurs from spring to autumn and that the spermatogenetic tissue is in a resting condition at other times of the year. He thus corrected the supposition of previous authors that spermatogenesis continues throughout winter, and added the information that living spermatozoa are stored in the epididymis of probably all of the species he studied with the exception of *Miniopterus schreibersii*. In the case of the last named species he stated that spermatozoa are not abundantly present in the males after November, although a few were found in the male genital tract of April specimens.

Nakano (1928), without knowledge of Courier's work, likewise found the sexual cycle of the males of the Japanese species *Vespertilio abramus* to be of the usual type described by Courier. Nakano stated that spermatogenesis begins at the end of spring and is complete in October. From the end of October to June the seminiferous tubules are in repose, but spermatozoa are stored in the tail of the epididymis from October to May.

While a periodic sexual cycle occurs in the male *Tadarida cynocephala*, spermatozoa are not stored in the epididymis for long after they cease to be produced in the testis, and the season when spermatogenesis occurs is different from that of the species of bats studied by Courier and Nakano. In figure 4, the presence or absence of spermatozoa in the testis or epididymis of specimens taken at various times of the year is indicated together with the weight of these organs after having been preserved in 10 per cent formalin.

The sections show that spermatozoa are abundantly present in the testis and epididymis of adult males taken in February and March, but none are present in these organs later in the year than April 18. From May to August, the seminiferous tubules are in a resting condition and no spermatozoa are stored in the epididymis. A proliferation of the spermatogenetic tissue takes place in September, resulting in an increase in the size of the seminiferous tubules and the testis as a whole. Spermatogenesis continues throughout the winter but no spermatozoa were found in specimens taken earlier in the winter than January 20. A few possibly mature spermatozoa are present in the testis of a specimen taken January 20, and another January 30, but no spermatozoa are present in the epididymis of these specimens.

It is thus evident that the male *Tadarida cynocephala* is sexually active only from early February to the middle of April, and that spermatozoa are not stored in the epididymis of this species for an unusually long time.

Courier and Nakano each showed that the accessory sex glands of the species of bats that they studied are well developed in males in which spermatozoa are present. That similar conditions exist in *Tadarida cynocephala* is shown by measurements of the length of the prostate gland, taken along

the mid-ventral line, as recorded in figure 5. These measurements were made on the same specimens in which the testis was studied. A comparison of figures 4 and 5 shows that the prostate gland is enlarged only when spermatozoa are present and that the enlargement of this gland occurs somewhat later than that of the testis. According to Courrier, the interstitial tissue of the testis is responsible for the regulation of the development of the accessory sex glands.

Males of *Tadarida cynocephala* in which the testes are small and contain no spermatozoa were taken in all months of the year. The prostate glands of the same specimens are also small. Of such individuals taken in the first 3 months of the year, the teeth are not greatly worn. For this reason it seems probable that the 'sexually immature males of this species taken during the breeding season are young. Probably they become mature in their second year.

The breeding habits of *Tadarida cynocephala* are apparently much like those of *Tadarida mexicana*, for Hartman (1933, p. 191) stated that Cuyler and himself found that the breeding season of the latter species occurs only in spring, the organs of both sexes being in a resting stage at other seasons.

Parturition in captive specimens of *Tadarida cynocephala* was observed in its entirety in 2 cases, but only one can be considered as normal. The other bat was weak and the young was dead when born. The last stages of parturition were observed in another captive. The observations of the birth of a normal young one were made June 30, 1931. The mother had been hanging head down from the side of the cage in the normal manner when she became restless and uttered a few notes, as this species usually does when irritated. It was then noticed that the fetus had changed from the transverse to the longitudinal position since the previous observation made 15 minutes earlier. A few minutes later the young appeared, rear end first, only 60 seconds elapsing from its first appearance until all but the head had emerged. During the brief pause, about 30 seconds, before the head emerged, the amnion was scratched to shreds by the claws of the mother's feet. The tail and feet of the young became extended, but it did not move at this time. The posture of the mother during parturition was not much different from that usually assumed by this species, and the flight membranes were not used to receive the young. As a result, immediately after birth, the young was suspended only by the umbilical cord. The mother seemed to ignore it completely and it was about 15 minutes before the young one found a nipple and began to nurse.

The placenta appeared about 2 hours after the birth of the young. At this time the mother tried to crawl away from the young one, which had hung up on the side of the cage beside its parent. The young, which was still attached by the cord, made no attempt to follow. After several such movements on the part of the mother, the placenta emerged. She went to

the opposite side of the cage and remained away from the young one until sundown. The placenta remained attached to the young by the cord for 2 days, when the dried cord broke close to the body.

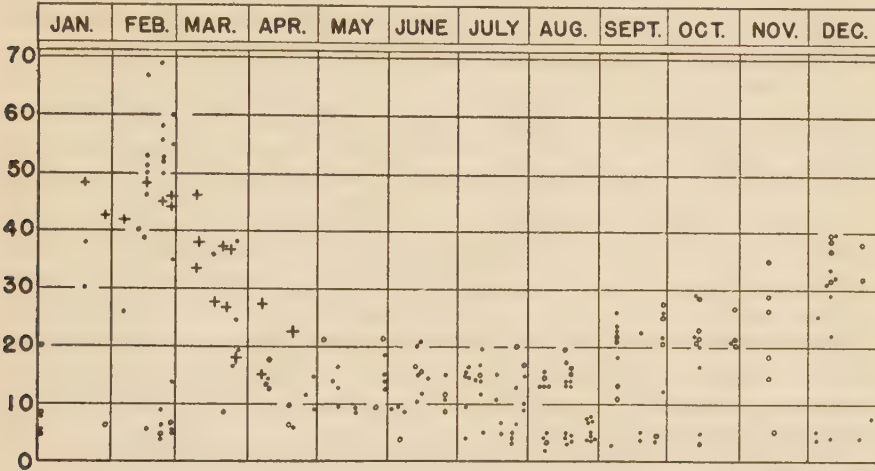


FIG. 4. Weight, in milligrams, of the testis of *Tadarida cynocephala*. Dots indicate organs which were not examined for the presence or absence of spermatozoa. Crosses indicate those in which spermatozoa were found to be present, and circles, those in which no spermatozoa could be found.

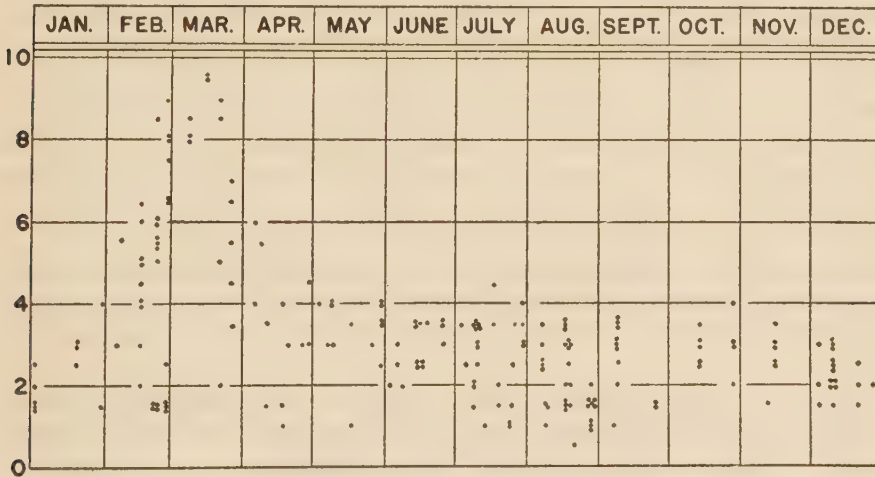


FIG. 5. Length, in millimeters, of the prostate gland of *Tadarida cynocephala*

Observations of the last part of parturition in another captive were made June 24, 1931. At 12:15 P. M. the fetus was in a transverse position, but when next observed at 12:40 all but the head of the young had emerged.

The amnion was torn and the young seemed much more vigorous than in the case of the one previously described. Its feet had found support on the side of the cage before parturition was complete and within 5 minutes after birth it was nursing, although, as in the former case, the mother had paid it no attention since its arrival. In this case the placenta was removed as described above half an hour after the birth of the young.

That the placenta is not devoured by the mother in this species, as is usually the case with mammals, is shown by the fact that the placenta remained attached to the young by the cord from 8 hours to 2 days in captives, and hundreds of young were observed in the colony with the placenta similarly attached. Apparently the time when the cord is broken depends largely on how much agitation it receives from the young and its associates.

Published information concerning parturition in bats has been found for 5 other species, all of which, so far as known, are members of the family Vespertilionidae. Birth of the noctule was described by Daniell (1834, p. 131) and Whitaker (1905, p. 327). Jobert ((1872, pp. 138-9) and Rollinat and Trouessart (1896, pp. 230-231) described the birth of the murin. Blake (1885, pp. 449-450) gave an account of parturition in a captive West Indian bat of unknown identity. He stated his intention of forwarding a couple of preserved specimens to the Science and Art Museum, Dublin. However, at my request, Dr. P. O'Connor, Keeper of the Natural History Division of the National Museum of Ireland, generously made a search for these specimens but without success. Parturition in *Myotis austroriparius* was described by Sherman (1930, pp. 496-497), and that of *Myotis lucifugus lucifugus* by Mohr (1933, pp. 52). From these accounts it seems that the vespertilionids regularly use the flight membranes, especially the interfemoral membrane, to receive the young at the time of birth. Also, the placenta is eaten and the cord broken by the mother in 4 of these 5 species. In *Myotis l. lucifugus*, however, Mohr stated that in several cases at least the cord was not severed but remained attached to the placenta, which dried, and that the cord broke off at the umbilicus on the second day.

The small size of the interfemoral membrane of the Molossidae in comparison with its extent in the Vespertilionidae furnishes a ready explanation for a lack of its use in *Tadarida cynocephala* as a receptacle for the young at birth.

From the evidence available, failure of the mother to devour the placenta and to break the cord may probably best be considered as specific peculiarities of *Tadarida cynocephala* and *Myotis l. lucifugus*.

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